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## FACTORS AND UNIT CHARACTERS IN MENDELIAN HEREDITY

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THE factorial hypothesis has played an important rôle in Mendelian heredity, and while students of Mendel's principles have had on the whole a pretty clear idea of the sense or senses in which they have made use of factors or symbols, yet those not engaged in the immediate work itself have, I believe, often been misled in regard to the meaning attached to the term factor, and by the assumed relation between a factor and a unit character. The confusion is due to a tendency, sometimes unintentional, to speak of a unit character as the product of a particular unit factor acting alone, but this identification has no real basis. It has, in fact, more than once been repudiated, yet the confusion has been so persistent that I venture to try to make clear my own position at least—it is one I think with which in the main many students of heredity will agree—in regard to the relation between unit-factors and unit-characters. I shall do this by means of several examples taken from my breeding experiments with the fly, *Drosophila ampelophila*.

The eye of this fly is red. A mutant arose with a vermillion eye. Crossed to the wild or red-eyed fly, the new color proved to be a Mendelian recessive.

According to the scheme that Mendel followed, red, *R*, and vermilion, *V*, are symbolized as complete and contrasting characters carried by the germ-plasm of the hybrid. They are assumed to separate in the germ-cells, and as a consequence two kinds of these cells are produced.

According to a more modern interpretation, known as the presence and absence theory, vermilion is supposed to arise through the loss of something from the germ-plasm of the wild fly. This something is not supposed to be the factor for vermilion, but another factor. On this scheme the red eye would be represented by the letters *RV*, and the vermilion eye by *rV*; as though the vermilion color arose through the loss of a red factor.

The relative advantages of these two modes of representation become apparent when two pairs of factors are involved. For instance, a new eye color—pink—appeared as a mutant. It, also, was recessive to red. Mendel's scheme would make the pink character the mate of the red character, just as vermilion had been before. But if pink and vermilion were mated to each other, it is not clear whether vermilion and pink should be treated as contrasted characters, or whether each should still be treated as allelomorphic to red. If either of these alternatives is adopted, the scheme fails to account for what actually happens. Mendel did not meet with such a situation, for none of his paired characters involved two changes in kind in the same organ, and consequently the problem did not exist for him.

Bateson did meet with just this situation in the case of the comb of fowls and the coat color of mice. His scheme, if applied to the present case of the eye colors in *Drosophila*, would be to represent red by *RV*, vermilion by *rV*, and pink by *Rv*. This scheme illustrates first why when vermilion is bred to pink a red-eyed fly, *rVRv*, should result; second, why in the second generation the proportion 9:3:3:1 should appear;<sup>1</sup> and third why in the eye

<sup>1</sup> Except in so far as modified by sex-linkage.

color series a new color is expected in the  $F_2$  generation, represented here by *rv*. This new color I called orange, and since *rv* only meant two absences, I followed the conventional method and added the symbol *O* to stand for orange. The completed formulæ were:

<i>RVO</i>	red
<i>rVO</i>	vermilion
<i>RvO</i>	pink
<i>rvO</i>	orange

This is identical with the scheme that Bateson adopted for the mouse color series, viz:

<i>GBCh</i>	gray
<i>gBCh</i>	black
<i>GbCh</i>	cinnamon
<i>gbCh</i>	chocolate

In a later paper (1912) I used the symbol *P* instead of *R*, so that the series stood:

<i>PVO</i>	red
<i>pVO</i>	vermilion
<i>PvO</i>	pink
<i>pvO</i>	orange

Let us now examine some of the possible interpretations of these symbols to see in what sense the letters were used for factors.

It is undoubtedly *implied, on the presence and absence scheme*, that something is *lost* from the original germ-plasm *PVO* when the vermilion *pVO* arises. The vermilion color is supposed to be the product of what is left when this something (called *P*) is lost. It is not supposed on this hypothesis that the vermilion factor alone is responsible for the vermilion color, for it is hypothetically only a part of what is left when something (*P*) is lost. Yet it is the identification of the vermilion factor with the vermilion eye-color that the opponents of Mendelism seem anxious to impute to the Mendelians.

Again, when the pink eye mutant appeared, it would have been assumed, on the presence and absence theory, that something was lost, so that the formula is  $PvO$ . Here again the pink color is the result of all that is left when something ( $V$ ) is lost. Pink is not assumed to be produced by a factor  $P$ , but by what is left when a factor  $V$  is lost. An egg is supposed to have lost something and vermilion developed, another egg is assumed to have lost something else and pink developed. It was the loss of the vermilion factor that allowed pink color to develop, and the loss of the pink factor that allowed vermilion color to develop. When pink and vermilion are mated together, the original color—red—is restored, because on this scheme what each has lost is made good by what is found in the other.

To my series of eye color factors the letter  $O$  was added to indicate the nature of the color produced when two factors,  $P$  and  $V$ , were assumed to be absent. The symbol  $O$  at that time did not seem to stand in the formulae on the same footing as  $P$  and  $V$ , because it stood for a color, and not for a factor that had been lost from the germ-cells of the wild fly. But since on the presence and absence scheme  $O$  stood for the residuum after  $P$  and  $V$  were lost it stood for the same sort of thing as did  $P$  and  $V$ , for  $P$  and  $V$  also stood for residua, *when they were not used as symbols for factors*. This will be made clearer later.

When the experiments had progressed to this stage, a new eye color appeared that was called eosin. Mated to orange it gave red; therefore, it seemed that this mutant must have contained  $P$  and  $V$ , and I inferred that it owed its color to the loss of an imaginary  $O$  factor. Eosin was represented, therefore, by  $PVo$ . But a moment's thought will show that on this scheme, *as long as  $P$  and  $V$  are present, any loss from the germ-plasm (giving a new eye color) added to orange should give red, because orange would contain what the new mutant had lost.*

The history of this case will show how, with the best of

intentions, one may be led into a paradoxical position in regard to the use of factors. Even admitting that the representation is purely symbolic, the letters used may unintentionally come to stand for different things. Thus in the case first cited, the letter  $P$  in the formula  $vP$  stood for a *residuum* that gave pink, but in the formula  $Vp$ , the letter  $p$  stood for the loss of a  $P$ -factor, yet  $p$  is the allelomorph of  $P$ , which latter, as stated, meant the residuum when  $V$  was lost. In other words, a double meaning was attached to  $P$ , for it stood both for the  $P$ -factor, which was only a part of the residuum, and also for the residuum as a whole. It is this doubleness of meaning that gives the opponents of Mendelian inheritance an occasion to impose upon the factorial hypothesis a meaning that is really foreign to it. Admitting that the Mendelians themselves have not always taken the pains to state explicitly that the symbols represent both a factor and a residuum, there is still little or no justification in imputing to the presence and absence theory the view that a given character, pink color, for instance, is the product of a pink factor alone. The attempt to impute to the factorial hypothesis the same interpretation that Weismann made use of in his theory of determinants rests largely upon an erroneous understanding of the symbolism employed. Weismann identifies each character of the organism as the product of a special determinant. The factorial hypothesis assumes only that the cell in one case is different from the cell in the other, the difference relating, it is true, to some part, but the character produced may be the result of the whole or of much of the cell, and not of one part alone.

There is a further difference between these two points of view. A change in a factor may have far-reaching consequences. Every part of the organization capable of reacting to the new change is affected. Though we seize upon the most conspicuous difference between the old type and its mutant, and make use of this alone, every student of heredity is familiar with cases where more

than the part taken as the index is affected. Weismann's theory, on the other hand, seems as a rule to identify each character with a special determinant for that character, and his meaning is clear when it is remembered that the process of development on Weismann's view is a process of sorting out of the determiners of the germ-plasm into different regions of the body. The factorial hypothesis makes no such assumption, but refers differentiation to the interaction of the parts on each other—every cell retaining the full complex of the original germ-plasm. Hence the possibility of the far-reaching effects of any change in the germ-plasm!

## II

The presence and absence *system of nomenclature* (aside from its implications as to what is meant by presence and absence) has till the present time justified itself, when properly interpreted, by its usefulness. It seems to me that as a system of nomenclature it may be used, if one so desires, quite apart from the idea, that a loss in a character involves necessarily a loss in the germ-plasm. I can bring forward one clear case at least that seems to me difficult to explain if absence is taken literally to mean the loss of a factor from the germ complex. I refer to a mutation "backwards," which in the older terminology meant reversion, or atavism.<sup>2</sup> In my pure cultures (at rare intervals) individuals have appeared like the original progenitors of the stock. I have not scrupled to put aside this evidence, because contamination, even with extreme care, will occasionally occur; and even if a reversion had occurred there would be no way of proving that it was such and not contamination. In fact, eosin first appeared in white-eyed stock and seemed to arise through reversion, but at the same time it seemed so improbable that this could happen that I tried to account for its appearance in a roundabout way. Now I should say that the factor *w* reverted to *W*.

<sup>2</sup> It is needless to add, perhaps, that atavism by recombination is not here for a moment brought into question.

But the clear case referred to above is the following: Quite recently there appeared in a culture bottle that had been producing for more than four months (probably for twelve generations) only wingless flies, an individual with one "wingless" wing and one normal wing on the other side. Here the evidence is conclusive that reversion had occurred. The wingless stock in which the asymmetrical form arose had purple eyes and the same eye color was present in the new type. As the eye color was relatively new at the time the chance that contamination had occurred was rendered very unlikely. Had contamination by a red-eyed fly occurred, making the new type a heterozygote, the eye color would have been the dominant red. When the asymmetrical fly ( $\sigma$ ) was bred to wingless females only wingless flies appeared, for three or more generations. The reversion, therefore, was somatic and did not involve the germ-plasm, yet this fact does not invalidate the question here raised.

In the light of this evidence, as well as the evidence from ever-sporting varieties (that may also be considered, I think, as mutating and reverting as regular processes), I believe it unwise to commit ourselves any longer to a view that a recessive character is necessarily the result of a loss from the germ-cell. We need only assume that some readjustment occurs, and as the result a new factor is produced. A simile may make this clearer, if not taken too literally. If we suppose that a factor is a labile aggregate, and that a rearrangement in it occurs, then the new aggregate in connection with the other parts of the cell produces a character that differs from the old one. Here there need be no loss, but only a change in configuration with a corresponding change in the end product in which the changed part plays a rôle, along with the other parts of the cell. A factor, in this sense, may exist in two or more forms according to the state of equilibrium; one of its states is dominant-producing, and the other is recessive-producing. Such a view may make it easier for us to appreciate that a mutation need

not be a loss, and that a recessive may revert in the sense that it may mutate. In chemical terms, the process is reversible.

### III

As I have pointed out, the presence and absence nomenclature, if properly understood, offers no practical difficulties so long as only two changes in the same organ are involved, but in experiments with *Drosophila* we have passed beyond this stage and must have at command a system by means of which more than two factors may be easily and conveniently represented. How impossible it becomes to use the presence and absence nomenclature when new characters are appearing may be shown by the following illustrations.

As already stated, Mendel's method of representing the allelomorphs sufficed so long as one new character is contrasted with the original one. In this sense the relation of a vermilion-eyed mutant to the red-eyed fly could be fully represented by treating red (*R*) and vermilion (*V*) as allelomorphs. But when another mutation in eye color appeared the scheme was no longer feasible. Now, in the same sense in which it became necessary to supplant Mendel's scheme by another one, it becomes necessary to change the presence and absence scheme when a third mutation appears in the same organ; for, the presence and absence scheme is not sufficiently elastic to allow the introduction of a new term in the series, unless a complete revision of the method is made each time that a new mutation in kind occurs.

For example, when it becomes desirable to compare the eosin eye with the vermilion-pink (or orange eye already known) it becomes puzzling to know what symbols to adopt. If, as I assumed, the symbol *O* in *VPO* is changed to small *o*, then the formula for eosin becomes *VPo*. But this is inconsistent with the scheme already adopted because the small letter *o* stands for a character called eosin. If to avoid this ambiguity a letter *E* (or *e*) is introduced for eosin the situation is even more puzzling.

The only logical method that could be followed, if an attempt is made to apply consistently the current scheme of presence and absence<sup>3</sup> would be the following:

When it becomes necessary to construct a series, let us say one involving three characters (*PVE*), the three double recessives (*Pve*, *pVe*, *pve*) must be made up and suitable names given to them, the initial letters of these names then become the factors sought. Such a procedure not only involves holding in suspense the naming of the factors until all the double recessives have been obtained, but involves renaming all the factors, each time a new series is made up.<sup>4</sup> This method is not likely to recommend itself if a simpler one can be employed. The plan here advocated avoids such difficulties.

The first letter (or the first and second or some other significant letter) of the name of the new character stands, as heretofore, as its symbol; thus *P* stands for the pink factor and small *p* stands for the correlative factor of the pink-eyed fly. Whether small *p* represents the loss of the *P* factor, or a change in that factor when the pink eye appears, is immaterial. The large letter represents the dominant character in conformity with the current scheme.<sup>5</sup> The eye color series will then be:

Red	<i>PVE</i>
Vermilion	<i>PvE</i>
Pink	<i>pVE</i>
Vermilion-pink	<i>pVE</i>
Eosin	<i>PVe</i>
Eosin-vermilion	<i>Pve</i>
Eosin-pink	<i>pVe</i>
Eosin-pink-vermilion	<i>pve</i>

<sup>3</sup> It is the nomenclature that is here brought into question and not, for the moment, the underlying conception of presence and absence, for even in my scheme this conception might still be held if it seemed desirable to do so.

<sup>4</sup> When, as in the case of the mouse colors, all the members of the series are known, there is no difficulty in finding suitable symbols, for the current names of the characters give the letters for the symbols.

<sup>5</sup> When a new *dominant* character appears it is represented by the capital letter and its allelomorph in the original form by a small letter.

The same scheme might be followed by using the small letters for the factors in the original red eye: thus red = *pve*; and the capital letter for the corresponding factor in the mutant; thus, vermilion = *pVe*, etc. A disadvantage of this scheme is that the large letter now stands for a recessive condition and the small letter (its allelomorph) for a dominant condition. Usage has, however, made us accustomed to interpreting a large letter as a dominant, its corresponding recessive (its allelomorph) by a small letter and therefore the plan first suggested seems more desirable. It is with much reluctance that I suggest this change in our present nomenclature. It has become necessary, however, in the case of the *Drosophila* to find some way to represent consistently those cases in which three or more factors are involved in the same organ. The change is not one of any theoretical importance, but a practical necessity for all cases of this kind. When one new character is contrasted with the original one, Mendel's way may still be the simplest and easiest way of formulating the results, and will, no doubt, be followed. When two new characters are involved the formula of presence and absence is a sufficient way of representing the symbols. But when new mutations are appearing some other plan must be adopted. The one here suggested has at least two merits: it is as easy to use as either of the foregoing for one and for two characters, and can also be utilized when any number of further mutations appear in the same organ.

The scheme applied to body colors is as follows: Two mutants arose, yellow and black, and by recombination, a "brown" or yellow-black fly was obtained. The symbols would be wild fly = *YYBB*, yellow = *yyBB*, black *YYbb*, and yellow-black *yybb*. Two other mutations in body color have appeared, both dark, one is called ebony, *eb* and the other sable, *s*. When brought in connection with the preceding mutation the gametic symbols would be:

Wild fly	<i>YBE<sub>b</sub>S</i>
Yellow	<i>yBE<sub>b</sub>S</i>

Black	$YbE_bS$
Yellow-black	$ybE_bS$
Ebony	$YBe_bS$
Sable	$YBE_bS$
Etc.	

Another combination is represented by certain wing mutations. A mutant called miniature appeared and may be represented by  $m$ ; another mutant appeared, called rudimentary, and may be represented by  $r$ ; and a third form, produced by recombination, was called miniature-rudimentary,  $mr$ . The symbols for this series would be:

Wild fly	$MR$
Miniature	$mR$
Rudimentary	$Mr$
Rud.-min.	$mr$

Later several other mutations in wings also appeared. Six of these may be selected for illustration, viz: Vestigial,<sup>6</sup>  $v_g$ ; Bifid,  $b_i$ ; Arc,  $a_r$ ; Curved,  $c_r$ ; Jaunty,  $j$ ; Balloon,  $b_a$ . If these are brought into connection with the foregoing the symbols for the wild fly in terms of these factors would be:

$$\text{Wild Fly} = M, R, V_g, B_i, A_r, C, J, B_a.$$

In order to study the relation of these characters to each other it has become necessary to combine many of them and in order to represent the results some system of symbols must be adopted. Obviously, it would be highly undesirable to be obliged to revise the system each time that any of these new mutations are brought into relation with those that have already been compared.

It may be asked, why may not the current scheme be retained, since in most cases only two characters are likely to be involved and characters can always be contrasted in pairs on this scheme? The answer is that more

<sup>6</sup> This is the wingless fly of former papers.

characters in the same organ have already been obtained, and it is at least as important to have a scheme by which they can be represented as it is to have a scheme where two characters only are studied. Moreover, the more characters that are obtained that show association in inheritance the further we may hope to go in our analysis of the constitution of the germ-plasm, which is admittedly the fundamental problem in the study of heredity. We must have some convenient way of representing the symbols in order to carry out this analysis, and on the grounds of convenience alone some scheme other than the current one must be found, at least for such a case as this of *Drosophila*. Another scheme has, in fact, been adopted by Baur and Hagedoorn. The letters that stand for the factors bear no relation to the name of the characters involved. This scheme allows the addition of any number of new factors to a series under consideration. In practise, however, this plan makes it extremely difficult to understand what any formula means without continual reference to the key of symbols used. We have found in practise that the scheme is so puzzling when several factors are under consideration that we have been led to follow the current method of representing each factor by the initial letter (or other suggestive letters) of the character that it stands for. Except in this regard the method of formulation here suggested is similar in principle to the A.B.C. scheme of Baur.

VERTICAL DISTRIBUTION OF THE CHÆTOG-  
NATHA OF THE SAN DIEGO REGION IN  
RELATION TO THE QUESTION OF  
ISOLATION VS. COINCIDENCE

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INTRODUCTION

EVER since Jordan ('05) called attention to the almost universal neglect of Moritz Wagner's contention that geographical isolation is an important factor in the formation of species, "Jordan's Law" ('05, p. 547) that "given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort," has been subject to much controversy and diversity of opinion. The conclusions of those biologists dealing with land fauna have, as a rule, emphasized the fact of isolation, whereas those of the marine biologist have tended to emphasize the fact of coincidence, or at least to doubt the truth of isolation. It is therefore part of the business of the marine biologist, through whose investigations new and important data have been accumulated, to throw as much light as possible upon the problems of isolation and coincidence. This is particularly true with regard to data concerning the Chætognatha because, as pointed out by Kofoid ('07), the group is exclusively marine and pelagic, and so completely circumscribed as to make it probable that their entire evolution has taken place within the confines of the open sea.

At the outset, the fundamental differences in the problem with reference to land and marine fauna must be emphasized. Kofoid ('07, p. 241) has pointed out that

"barriers are far less in evidence in the environment of the pelagic fauna than in that of the shore or of the land," and that, while there do exist "limited regions along the margins of great ocean currents" which might afford means of hydrographic isolation, changes in hydrographic conditions such as temperature, density, substances in solution, illumination, etc., are so gradual that stratified areas do not exist to any large extent. Furthermore, land faunas are segregated into neighboring or remote areas almost entirely with reference to latitude and longitude. With pelagic faunas this is not necessarily, perhaps not usually, the case, for a third dimension—*depth*—is involved. It therefore follows that closely related pelagic organisms may be *coincidentally distributed as regards latitude and longitude, and still be completely isolated in their vertical distribution.*

This fact signifies that data respecting the isolation of a pelagic fauna will be wholly inadequate unless the vertical distribution of the particular species or group under consideration be capable of determination and analysis. In his discussion of "the coincident distribution of related species of pelagic organisms as illustrated by the *Chaetognatha*" Kofoed ('07), while recognizing the force of this point, has utilized data pertaining almost exclusively to latitude and longitude. This was consequent upon no lack of appreciation on his part of the real problem involved, but solely to the fact that the necessary data were missing. Moreover, what little has been previously discovered relative to the vertical distribution of this group was based upon observations scattered over such large areas as to make any approach to critical analysis of the problem of isolation almost impossible. However, through the efforts of the San Diego Marine Biological Station, a mass of data has been collected which enables an entirely new light to be thrown upon this problem.

Since 1904 this station has centered its collecting upon an irregular area of about 30 square miles lying be-

tween  $32^{\circ} 20'$  and  $33^{\circ} 30'$  N., and between the coast and  $119^{\circ}$  W. From this small area 68,962 specimens comprising ten species of Chætognatha have been collected, and, as all depths between the surface and 350 fathoms have been examined with horizontal closing nets, the depth from which each specimen was obtained is known with the nearest approach to certainty permitted by any known method of collecting. As a critical analysis of this data has been published elsewhere [see Michael ('11)] reference must be made to that paper for the methods, problems and details involved in determining the vertical distribution of each species, so that, in the following pages, only the fruits of that research bearing directly upon the present subject-matter will be discussed. It will be shown (1) that of the most closely related "couplets" of species only one has been taken from the San Diego region, (2) that, of those species occurring in this region, each has its own definite and *specific* manner of vertical distribution, (3) that the most diverse species (morphologically) have the most coincident vertical distribution, and (4) that, while several species have sometimes been taken in the same haul, rarely more than one was represented by sexually mature individuals.

#### RELATIONSHIPS BETWEEN THE SPECIES OF CHÆTOGNATHA

Adopting Ritter-Záhony's ('11 b) careful revision of the Chætognatha as our starting point, the group becomes separable into six genera, *Sagitta*, *Pterosagitta*, *Spadella*, *Eukrohnia*, *Heterokrohnia* and *Krohnitta*. *Sagitta* is represented by eighteen valid and four rather doubtful species, *Pterosagitta* is represented by one, *Spadella* by one, *Eukrohnia* by two, *Heterokrohnia* by one and *Krohnitta* by two.

Now the eighteen valid species of *Sagitta* fall into two sharply contrasted groups by virtue of the presence or absence of a *collarete* which is a conspicuous thickening of the epidermis posterior to the head. Ten species are

provided with this structure, while in eight it is entirely missing. The species comprising each group are listed below:

<i>Species with Collarette</i>	<i>Species without Collarette</i>
<i>S. bipunctata</i>	<i>S. enflata</i>
<i>S. decipiens</i>	<i>S. hexaptera</i>
<i>S. neglecta</i>	<i>S. lyra</i>
<i>S. regularis</i>	<i>S. gazelle</i>
<i>S. ferox</i>	<i>S. serratodentata</i>
<i>S. planktonis</i>	<i>S. bedoti</i>
<i>S. hispida</i> ( <i>robusta</i> Doncaster)	<i>S. elegans</i>
<i>S. tenuis</i>	<i>S. macrocephala</i>
<i>S. pulchra</i>	
<i>S. siboga</i>	

Those species having the *collarette* may be further separated into diverse groups by means of the following *main* characteristics: (1) Those in which the body is transparent as contrasted with those in which it is opaque, (2) those in which the collarette extends to the ventral ganglion as contrasted with those in which it never extends more than half way to the ganglion, (3) those in which the anterior fin extends to the ventral ganglion as contrasted to those in which it does not, (4) those having more than 50 per cent. of the posterior fin in front of the tail-septum as contrasted with those having more than 50 per cent. of the fin behind the tail-septum, and (5) those in which the anterior fin is shorter than the posterior fin as contrasted with those in which the posterior fin is the shorter. Let it not be thought that these are the only characteristics used to differentiate the various species of *Sagitta* provided with the *collarette*. Far from it! Many others of great specific importance are made use of, but, if classified according to those just enumerated, the most closely related "couplets" remain inseparable while those species not so closely related are readily separated from each other. This may be graphically represented by arranging these five pairs of contrasted characteristics into a series of "rows" and

"columns" and then writing the names of the species, having those in question in each square made by the intersecting "arrays." Such an arrangement is given below:

TABLE I.

	More than 50 Per Cent. of Posterior Fin in Front of Tail-septum	Less than 50 Per Cent. of Posterior Fin in Front of Tail-septum	Anterior Fin Shorter than Posterior Fin	Anterior Fin Longer than Posterior Fin
Body transparent.	<i>S. bipunctata</i> <i>S. decipiens</i> <i>S. pulchra</i>	<i>S. tenuis</i>	<i>S. bipunctata</i> <i>S. decipiens</i> <i>S. tenuis</i>	<i>S. pulchra</i>
Body opaque.	<i>S. planktonis</i> <i>S. sibogæ</i>	<i>S. neglecta</i> <i>S. regularis</i> <i>S. ferox</i> <i>S. hispida</i>	<i>S. neglecta</i> <i>S. regularis</i> <i>S. hispida</i>	<i>S. planktonis</i> <i>S. ferox</i> <i>S. sibogæ</i>
Collarette extending to ventral ganglion	<i>S. planktonis</i>	<i>S. neglecta</i> <i>S. regularis</i> <i>S. ferox</i>	<i>S. neglecta</i> <i>S. regularis</i>	<i>S. ferox</i> <i>S. planktonis</i>
Collarette not extending over half way to ventral ganglion.	<i>S. bipunctata</i> <i>S. decipiens</i> <i>S. pulchra</i> <i>S. sibogæ</i>	<i>S. hispida</i> <i>S. tenuis</i>	<i>S. bipunctata</i> <i>S. decipiens</i> <i>S. hispida</i> <i>S. tenuis</i>	<i>S. pulchra</i> <i>S. sibogæ</i>
Anterior fin extending to ventral ganglion.	<i>S. planktonis</i> <i>S. pulchra</i> <i>S. sibogæ</i>	<i>S. neglecta</i> <i>S. regularis</i> <i>S. ferox</i> <i>S. tenuis</i>	<i>S. neglecta</i> <i>S. regularis</i> <i>S. tenuis</i>	<i>S. ferox</i> <i>S. planktonis</i> <i>S. sibogæ</i> <i>S. pulchra</i>
Anterior fin not extending to ganglion.	<i>S. bipunctata</i> <i>S. decipiens</i>	<i>S. hispida</i>	<i>S. bipunctata</i> <i>S. decipiens</i> <i>S. hispida</i>	

An examination of this table shows that in every square where *S. bipunctata* occurs there also *S. decipiens* is found, and the same relation holds between *S. neglecta* and *S. regularis*. These four species, then, are to be regarded as constituting two very closely related "couplets." A third "couplet," whose constituent species are somewhat less closely related, is that of *S. ferox* and *S. planktonis*, which only differ in the proportional extent of the posterior fin in front of the tail-septum. The remaining species are clearly distinct.

Turning attention to those *Sagitta* devoid of the collarette, *S. enflata*, *S. hexaptera*, *S. lyra*, *S. gazellæ* and *S. bedoti* are exceedingly transparent, while *S. serrato-*

*dentata*, *S. elegans* and *S. macrocephala* are opaque. While the three opaque species are unmistakably distinct, we find that, in the transparent group, *S. enflata* and *S. hexaptera* form one closely related "couplet" while *S. lyra* and *S. gazellæ* make another. This is shown more clearly below:

TABLE II.

	Posterior Fin Extends Caudally to Seminal Vesicles	Posterior Fin Never Extends to Seminal Vesicles	Anterior Fin Confluent with Posterior Fin	Anterior and Posterior Fins Always Separated by an Interval
More than 50 per cent. of posterior fin in front of tail-septum.	<i>S. lyra</i> <i>S. gazellæ</i>	<i>S. enflata</i> <i>S. hexaptera</i>	<i>S. lyra</i> <i>S. gazellæ</i>	<i>S. enflata</i> <i>S. hexaptera</i>
Less than 50 per cent. of posterior fin in front of tail-septum.	<i>S. bedoti</i>			<i>S. bedoti</i>

All told, then, we have in the genus *Sagitta* five closely related "couplets" of species. It is not to be presumed that every "couplet" expresses the same degree of closeness between its two members, for such is not the case. Unquestionably the two species most closely related are *S. neglecta* and *S. regularis*, and the two least so—*S. ferox* and *S. planktonis*. Now if we list these "couplets" in one column and the species so far taken from the San Diego region in another, the interesting fact is evident that, except in one case, the San Diego *Sagitta* contain only one species of each "couplet." Such lists are given below.

*San Diego Sagitta*

*S. neglecta*  
*S. bipunctata*  
*S. lyra*  
*S. enflata*  
*S. hexaptera*  
*S. planktonis*  
*S. serratodentata*

## "Couplets"

*S. neglecta*-*S. regularis*  
*S. bipunctata*-*S. decipiens*  
*S. gazellæ*-*S. lyra*  
*S. enflata*-*S. hexaptera*  
  
*S. planktonis*-*S. ferox*

Looking to the other genera we find *Eukrohnia* composed of two species (*E. hamata* and *E. fowleri*), *Krohnitta* of two (*K. subtilis* and *K. pacifica*), and *Heterokrohnia*, *Pterosagitta* and *Spadella* of one each. Now *E. hamata* and *E. fowleri* form an exceedingly closely related "couplet," but only the former is known to occur in the San Diego region. Again, *K. subtilis* and *K. pacifica* are so nearly alike that it is very difficult to describe their differences although they are probably valid species. Yet, only the first has been found in California waters. Of the three remaining genera *Heterokrohnia* and *Spadella* are not represented in our collections, and *Pterosagitta* by only one individual of its single species *P. draco*.

In so far, therefore, as the relationships among the Chaetognatha have been correctly interpreted, it is evident that, except for the occurrence of both *S. enflata* and *S. hexaptera*, there is no instance of two of the most closely related species having been taken from the San Diego region.

#### GENERAL DISTRIBUTION OF THE "COUPLETS"

Having pointed out that only one of a "couplet" of the most closely related species occurs in the San Diego region, it will be interesting to ascertain to what extent the same relation holds in other parts of the world. Furthermore, wherever both members of a "couplet" are recorded from the same vicinity it will be to the point to determine, if possible, to what extent their distribution within the area is coincident or isolated.

#### S. NEGLECTA AND S. REGULARIS

The members of this "couplet" may be designated as warm water, epiplanktonic species whose northern and southern limits of distribution are 35° N. and 9° S. The highest surface temperature recorded in connection with their capture is 29° C. and the lowest 15°.5 C. They were both originally described by Aida ('97) from Misaki

Harbor, where, so far as known, they are coincidently distributed.

In the *Siboga* area Fowler ('06) records 45 surface hauls containing either one or the other species. Of these, 35 contained *S. neglecta* but not *S. regularis*, and 6 contained *S. regularis* but not *S. neglecta*. In only 4 hauls were both species obtained. When we remember the large area covered by this expedition these results point toward contiguous and slightly overlapping, rather than coincident distribution.

The two expeditions of the *Pola* to the Red Sea obtained both *S. neglecta* and *S. regularis*. The collections of the first expedition (1895/96) were made in an area limited by 21° 27' and 29° 45' N., and 32° 30' and 38° 30' E., while those of the second (1897/98) were made somewhat further south and east within the limits of 15° 1' and 28° 42' N., and 32° 56' and 42° 31' E. Ritter-Záhony ('09) records 32 surface hauls made during the first expedition that contained one or other of the two species. Of these, 25 contained only *S. regularis*, 6 only *S. neglecta*, while in but one haul were both species taken. During the second expedition 27 surface hauls were made of which 12 contained *S. neglecta* only, 10 *S. regularis* only, and 5 contained both. These data strongly suggest that the two species are distributed in contiguous regions which overlap considerably along the edges.

Of the other expeditions, the *Biscayan*, *Plankton* and *National* failed to catch either species. The *Gauss* obtained both in the region of Port Natal, but never in the same hauls. Doncaster ('02) records both under the names of *S. septata* and *S. bedfordii* from the Maldiva and Laccadive Archipelagoes, but nothing is stated as to whether they were obtained in the same hauls or not. Ritter-Záhony ('10a) records *S. regularis* from Sharks Bay, Australia, but failed to find *S. neglecta*.

## S. BIPUNCTATA AND S. DECIPiens

*S. bipunctata* is a eurythermal, euryhyaline and cosmopolitan species recorded from the epiplankton of the arctic, sub-arctic, north temperate, tropical and south temperate Atlantic Ocean, the south temperate and tropical Indo-Australian Ocean, and the north temperate Pacific Ocean, as well as from the mesoplankton of the north temperate and tropical Atlantic. Its northern limit is 74° N. and its southern 28° S. The highest temperature recorded in connection with its capture is 33°.6 C., while the lowest is 0°.2 C. *S. decipiens*, on the other hand, is mesoplanktonic. Both were taken from the Bay of Biscay, *S. decipiens* from between 100 and 200 fathoms, and *S. bipunctata* only in open vertical hauls made between 50 and 200 fathoms to the surface, the total yield being only 7 specimens. Ritter-Záhony ('10 b, p. 4) records both from the Irish Sea, but, in regard to *S. decipiens*, says: "*S. decipiens* is purely mesoplanktonic and in the Irish area was only found at depths varying from 164 to 1,150 fathoms." Concerning *S. bipunctata* he says that it is "confined to the epiplankton. . . . The quantity of *S. bipunctata* in the upper epiplankton is larger than in the lower." Finally, both species have been taken in the Atlantic Ocean between 60° N. and 8° S. but, while *S. decipiens* occurred only in open nets from below 100 fathoms and in closing nets from between 100 and 600 fathoms, *S. bipunctata* occurred only in the epiplankton. From this evidence it seems that wherever the two species occur in the same region they are isolated by their manner of vertical distribution.

## S. LYRA AND S. GAZELLE

*S. lyra* is a cold water, nearly eurythermal species ranging from 73° N. to 7° 33' S., the highest temperature recorded in connection with its capture being 18°.6 C. and the lowest 1°.1 C. It has been found in the epiplankton of the arctic, sub-arctic and north temperate Atlantic, and sub-antarctic Pacific Oceans, as well as in the meso-

plankton of the sub-arctic, north temperate and tropical Atlantic, the tropical Indo-Australian and the north temperate Pacific oceans. *S. gazellæ*, on the other hand, is a rare form. A few specimens were first taken during the *Gazelle* expedition from the Indian Ocean ( $43^{\circ}$  S.) from a depth of 75 and 1,300 fathoms. It is also recorded from the Atlantic Ocean ( $35^{\circ}.5$  S.), where it was taken in a single haul from about 1,400 fathoms, and from the Antarctic Ocean between  $60^{\circ}$  and  $66^{\circ}$  S., where it was taken from 10, 25 and 50 fathoms. These data indicate that *S. gazellæ* is confined to the southern hemisphere and tends to be distributed circumpolarly. Records of the *Gauss* expedition show that out of 88 hauls containing either *S. lyra* or *S. gazellæ*, 39 contained only the former, 42 only the latter, and 7 both species.

#### S. ENFLATA AND S. HEXAPTERA

*S. enflata* is a warm water purely epiplanktonic species whose northern and southern limits of distribution are  $40^{\circ} 24'$  N. and  $34^{\circ} 52'$  S. The highest temperature recorded in connection with its capture is  $32^{\circ}$  C. and the lowest  $15^{\circ}.5$  C. It has been taken from the north temperate, tropical and south temperate Atlantic, the south temperate and tropical Indo-Australian and the north temperate Pacific oceans. *S. hexaptera*, on the other hand, is a eurythermal, nearly cosmopolitan species found in the lower epiplankton or mesoplankton of the arctic, sub-arctic, north temperate, tropical and south temperate Atlantic, the south temperate and tropical Indo-Australian and the north temperate and sub-antarctic Pacific oceans. Its northern and southern limits of distribution are  $74^{\circ}$  N. and  $28^{\circ}$  S., while the extremes of temperature recorded in connection with its capture are  $29^{\circ}$  C. and  $6^{\circ}$  C.

Both species have been taken together from the same areas during a number of expeditions. In the *Siboga* area Fowler ('06) records 58 surface hauls containing one or other of the species, of which 31 contained both,

while 26 contained *S. enflata* but not *S. hexaptera*, and only one contained *S. hexaptera* alone. During the first expedition of the *Pola* to the Red Sea 32 surface hauls were made which contained both species, 21 which contained *S. enflata* but not *S. hexaptera*, and only one which contained *S. hexaptera* alone. During the second expedition not a single *S. hexaptera* was taken in surface hauls that was not accompanied by *S. enflata*, there being 13 hauls containing both and 29 containing *S. enflata* alone. Finally, during several expeditions covering parts of the Adriatic, Ionian and Ægean seas, Ritter-Záhony ('08) records 45 surface hauls containing *S. enflata*, of which 6 also contained *S. hexaptera*, and only 4 hauls in which the latter species was taken without the former.

These data certainly indicate a high degree of coincidence. However, the fact that *S. enflata* is rarely reported other than from the upper epiplankton and that *S. hexaptera* is more typical of the lower epiplankton and mesoplankton, suggests isolation with respect to sexual maturity. Concerning this Ritter-Záhony ('10*b*), who has been very careful to distinguish immature from mature specimens, says: "Like *S. serratodentata*, *S. hexaptera* is a species which can not endure low temperatures until it has reached the adult stage. . . . We do not, as a rule, find large specimens until we come to the lower epiplankton." Until more is known regarding the stages of growth of these specimens taken on the surface together with *S. enflata* we can not regard the cases of coincidence revealed above as anything more than negative evidence of isolation.

#### S. PLANKTONIS AND S. FEROX

*S. planktonis* is a eurythermal species recorded from both epi- and meso-plankton of the north temperate Atlantic and Pacific oceans. It has not been reported north of 32° 45' N., nor south of 8° 30' S., except for a few small specimens from the Antarctic between 65° and

66° S. Its temperature range is from 27° C. to 4° 7 C. *S. ferox*, on the other hand, is a warm-water species confined, so far as known, to the epiplankton of the tropical Indo-Australian region. Both species were taken during the *Siboga* expedition, but, while *S. ferox* was taken in abundance from the surface, *S. planktonis* was taken only from the mesoplankton. There is no record of both having been taken in the same hauls except in those made with open vertical nets.

#### E. HAMATA AND E. FOWLERI

It is still an open question in my mind whether *E. fowleri* is a valid species or merely a synonym for *E. hamata*. Ritter-Záhony ('11 b) describes certain differences, but the characters used appear indicative of variation within the species rather than of constant specific characters. If they should prove synonymous, then *Eukrohnia* would be represented by only one species. However, assuming their validity, then *E. hamata* would be distributed in the mesoplankton of the Indian, Atlantic and Antarctic oceans, while *E. fowleri* is rarer and perhaps more cosmopolitan, occurring in the Irish sea between 200 and 1,100 fathoms, in the Bay of Biscay below 325 fathoms, in the Malay Archipelago below 460 fathoms, and rarely in the open Atlantic below 500 fathoms. It might be added that *E. hamata* also occurs in the epiplankton of the Arctic and Antarctic regions, while *E. fowleri* always remains confined to the mesoplankton. During the *Plankton* expedition the species were taken together in only one closing-net haul made between 500 and 600 fathoms, and only twice out of 18 open vertical hauls from a variety of depths.

#### K. SUBTILIS AND K. PACIFICA

*K. subtilis* is regarded as a eurythermal cosmopolitan species ranging from 60° 12' N. to 29° 30' S. The temperature corresponding to its capture varies from 30° 8

C. to  $5^{\circ}.3$  C. It is reported from both epi- and mesoplankton of the north temperate and tropical Atlantic and tropical Indo-Australian oceans, as well as from the epiplankton of the south temperate Atlantic and south temperate Indo-Australian oceans and from the mesoplankton of the north temperate Pacific. *K. pacifica*, on the other hand, is a warm-water epiplanktonic species from the tropical Atlantic and Indo-Australian, and the north temperate Pacific oceans. Its northern limit is  $35^{\circ}$  N. and its southern  $7^{\circ} 30'$  S. During the *Siboga* expedition both species were taken together in but one haul, and that one made by an open vertical net from 1,000 fathoms. This is the only instance, so far as I can ascertain, where both species have been obtained from the same area.

In summing up we find that the members of each "couplet" tend to be isolated in one way or another. *S. neglecta*, for instance, maintains a distribution which, while overlapping more or less, is contiguous rather than coincident with that of *S. regularis*. In the case of *S. bipunctata* and *S. decipiens* the data show that wherever both are taken within the same area the former is confined to the epiplankton, while the latter occurs only in the mesoplankton. With *S. lyra* and *S. gazelle* the distribution is never coincident, but, in some instances, contiguous and overlapping. *S. enflata* and *S. hexaptera* present the most striking evidence in favor of coincidence but, even here, the chances are that only the immature of *S. hexaptera* occur in the upper epiplankton, so that an effective physiological isolation is probably maintained. *S. planktonis* and *S. ferox*, while they do occur together in the *Siboga* area, are isolated by their manner of vertical distribution, *S. ferox* being epiplanktonic and *S. planktonis* mesoplanktonic. The members of the doubtful "couplet" comprising *E. hamata* and *E. fowleri* are only rarely taken in the same net hauls, which indicates contiguous rather than coincident distribution, although this appearance may be due entirely to the fact that *E. fowleri* is not abundant anywhere. Finally, *K. subtilis* and *K.*

*pacifica* have never been taken from the same region, excepting in the case of the *Siboga* expedition when they were obtained together in only one haul from 1,000 fathoms to the surface.

#### VERTICAL DISTRIBUTION OF THE CHÆTOGNATHA OF THE SAN DIEGO REGION

The 68,962 specimens of Chætognatha obtained from the San Diego region were distributed among the various species as follows:

<i>S. bipunctata</i> .....	51,670
<i>S. enflata</i> .....	10,127
<i>S. serratodentata</i> .....	6,575
<i>S. lyra</i> .....	271
<i>S. neglecta</i> .....	127
<i>E. hamata</i> .....	72
<i>K. subtilis</i> .....	50
<i>S. planktonis</i> .....	41
<i>S. hexaptera</i> .....	28
<i>P. draco</i> .....	1

Turning attention first to those species that must be regarded as visitants rather than residents of this region we find that *S. enflata*, *S. neglecta*, and the single specimen of *P. draco* were all obtained from the upper epiplankton mainly during February, 1905, when the surface temperature was 15°.5 C. One surface haul made on the morning of February 25 obtained 3,500 *S. enflata*, many of which were sexually mature, 9 immature *S. neglecta*, and the single very immature specimen of *P. draco*. A second surface haul, made the same morning, contained 3,100 *S. enflata* (most of them sexually mature) and 75 immature *S. neglecta*. Six more *S. enflata* and 38 immature *S. neglecta* were obtained in a surface haul made on April 29, 1905, and a seventh *S. enflata* in a surface haul made on June 11, 1908. Of the remaining *S. enflata*, 3,507 were obtained in open vertical hauls (from ten fathoms or less) during the fall of 1904, 3,500 having been taken in one haul. The five remaining *S. neglecta* were also obtained in the same haul, and the 13 *S. enflata*,

still unaccounted for, were all obtained in open vertical hauls from 45, 75, 110 and 290 fathoms.

These data indicate that these three species can not be regarded as typical of the San Diego region, and since they occur abundantly in the surface waters of more tropical seas where the temperature reaches 34° C., it seems likely that they have been carried here by currents from the warmer regions, although no such currents are known with certainty. The probability of this supposition is somewhat increased because of their reoccurrence here during the past winter after an absence of over two years.

Of the remaining species, *S. bipunctata*, *S. serratodentata*, and *S. lyra* are the most typical of the San Diego region. The number of each species obtained from the various depths with horizontal nets is shown in the following table:

TABLE III

TOTAL NUMBER OF SPECIMENS OBTAINED WITH THE HORIZONTAL NETS

Depth in Fathoms	<i>S. bipunctata</i>	<i>S. serratodentata</i>	<i>S. lyra</i>	Number of Hours of Hauling
0-25	30,733	93	5	108.1
25-75	275	106	20	11.0
75-150	10	106	20	6.5
150-250	0	174	17	3.1
250-350	0	43	54	5.4

This table reveals the fact that *S. bipunctata* was obtained in by far the greatest numbers between the surface and 25 fathoms, and that it was not taken at all below 150 fathoms. *S. serratodentata*, on the other hand, appeared in greatest abundance between 150 and 250 fathoms, and *S. lyra* between 250 and 350 fathoms. However, the mere tabulation of the number of specimens taken from the various depths does not reveal the true significance of the data, for it is obvious, from the last column, that the amount of hauling, and consequently the amount of water filtered, has varied with the depth so that the *relative* density or abundance in the various depths is not repre-

sented by the total number of specimens obtained. A more accurate and justifiable presentation is to express the total number of specimens obtained from each of the above depths in terms of the average number per unit of time consumed in hauling. The following table reveals this relative abundance of the three species as thus determined:

TABLE IV  
RELATIVE ABUNDANCE OR AVERAGE NUMBER OF SPECIMENS OBTAINED PER 20  
HOURS OF HAULING<sup>1</sup>

Depth in Fathoms	<i>S. bipunctata</i>	<i>S. serratodentata</i>	<i>S. lyra</i>
0-25	5,685	17	1
25-75	420	193	36
75-150	31	326	61
150-250	0	1,123	110
250-350	0	159	200

It is evident that this table brings into still more striking relief the fact that *S. bipunctata* is most abundant between the surface and 25 fathoms, from where it decreases in abundance as the depth increases, while *S. serratodentata* increases from a minimum between the surface and 25 fathoms to a maximum between 150 and 250 fathoms, and *S. lyra* increases from a minimum near the surface to a maximum in the deepest water (250 to 350 fathoms). While it is very improbable, owing to variations in many environmental conditions affecting the abundance of the three species in the various depths, that subsequent collecting would ever result in *exactly* the same averages as given above—it is just as improbable that, if the hauls were distributed in approximately the same manner, with regard to such environmental conditions, as those from which the above data were derived, we should find the relative abundance much altered. Consequently it is no exaggeration to say that *each of these three species has its own definite and specific manner of vertical distribution just as truly as each has its own*

<sup>1</sup> As relative abundance is independent of the particular unit of time selected for standardizing the data, a unit of 20 hours has been used instead of the more obvious 1 hour in order to eliminate fractions in the case of *S. lyra*.

*specific morphological characteristics*, and it would be quite as easy to identify the species from an analysis of data regarding its vertical distribution within an area *analogous* to the San Diego region as it would from the usual taxonomic descriptions.

Detection of specific differences in the vertical distribution of the remaining species is rendered more uncertain because so few specimens have been obtained. However, by taking the species one at a time, it will be seen that tendencies, at least, toward specification are revealed.

#### SAGITTA PLANKTONIS

Eliminating those catches made with open vertical nets as of little or no value in determining the depths from which specimens were obtained, we find that seven *S. planktonis* were taken between the surface and 150 fathoms, two between 150 and 200 fathoms, six between 200 and 250 fathoms, and eleven between 250 and 300 fathoms. If we separate those obtained with horizontal from those obtained with vertical closing nets the relative abundance of the species in these various depths may be expressed as in the following table:

TABLE V  
RELATIVE ABUNDANCE OF *Sagitta planktonis*

Depth in Fathoms	Horizontal Closing-Net Catches Showing Number of Specimens per 20 Hours of Hauling	Vertical Closing-Net Catches Showing Number of Specimens per 500 Fath- oms of Hauling
0-150	1	none
150-200	5	1
200-250	8	8
250-350	19	18

This table shows that this species increases in abundance as the depth increases and reaches its maximum in the neighborhood of 300 fathoms. When we realize that approximately the same relative abundance is obtained from independent considerations of data supplied by horizontal and vertical closing nets, this conclusion is placed upon solid ground, in spite of the few specimens dealt with.

## SAGITTA HEXAPTERA

Some indication of the relative abundance of this remaining species of *Sagitta* may be gleaned from the following table:

TABLE VI  
RELATIVE ABUNDANCE OF *Sagitta hexaptera*

Depth in Fathoms	Horizontal Closing-Net Catches Showing Number of Specimens per 100 Hours of Hauling	Vertical Closing-Net Catches Showing Number of Specimens per 1,000 Fathoms of Hauling
0-50	9	none
50-100	88	4
100-150	none	2
150-350	none	none

When to the evidence contained in this table we add that the species was not obtained in hauls made with open vertical nets from above 45 fathoms, the facts suggest that *S. hexaptera* maintains its maximum abundance between 50 and 100 fathoms. The number of specimens, however, is too small to afford basis for any more positive conclusion.

## KROHNITTA SUBTILIS

Regarding this species, we find that the horizontal closing nets obtained four specimens from 200 fathoms, but none from above or below this depth. The vertical closing nets, on the other hand, obtained twelve from between 50 and 200 fathoms, 25 from between 200 and 250 fathoms, and five from between 250 and 300 fathoms. Only three were obtained by the open vertical nets and those in one haul made from 250 fathoms to the surface. The following table gives a more accurate idea of the relative abundance of this species:

TABLE VII  
RELATIVE ABUNDANCE OF *Krohnitta subtilis* BASED ON VERTICAL CLOSING  
NET CATCHES

Depth in Fathoms	Average Number of Specimens per 1,000 Fathom Haul
0-50	none
50-200	18
200-250	63
250-300	20

The table indicates that *K. subtilis* maintains its maximum abundance between 200 and 250 fathoms, and all the data agree that it does not occur above 50 fathoms.

#### EUKROHNIA HAMATA

Two specimens of this species were taken with horizontal closing nets from 110 fathoms, two from 300 fathoms, and two from 350 fathoms. The vertical closing net obtained nine from between 25 and 50 fathoms, one from between 150 and 200 fathoms, six from between 200 and 250 fathoms, and one from between 250 and 300 fathoms. None were obtained in open vertical hauls made from above 250 fathoms. These data show that *E. hamata* is typical of the mesoplankton, and suggest that the region of maximum abundance is in the neighborhood of 250 fathoms.

The essential facts presented in this brief discussion of vertical distribution may best be summed up by classifying so far as possible the various species within the San Diego region on the basis of similarities and differences in their manner of distribution. When this attempt is made we find that a key somewhat as follows may be built up:

#### KEY TO THE SPECIES OF CHÆTOGNATHA OF THE SAN DIEGO REGION BASED ENTIRELY UPON FACTS OF DISTRIBUTION

- A. Species conspicuously epiplanktonic, very rarely extending to a depth of 150 fathoms .....B.
- AA. Species conspicuously mesoplanktonic, very rarely occurring above 100 fathoms .....E.
- B. Species confined to the upper 10 fathoms .....D.
- BB. Species whose depth of maximum abundance is below 10 fathoms .....C.
- C. Species occurring in large numbers and distributed from the surface to 75 fathoms, but occurring in much the greatest abundance between the surface and 25 fathoms...*S. bipunctata*.
- CC. Species not occurring in large numbers, the region of greatest abundance being at least below 40 fathoms.....*S. hexaptera*.
- D. Species occurring rarely, but in large numbers (1,000 or more per haul not being unusual) .....*S. enflata*.
- DD. Species occurring rarely and in very small numbers (more than 100 per haul being unusual) .....*S. neglecta*.

- E.* Species increasing in relative abundance as the depth increases, reaching a maximum at a depth of 250 fathoms or more. . . . . *F.*  
*EE.* Species increasing in relative abundance as the depth increases, but reaching a maximum between 150 and 250 fathoms. . . . . *G.*  
*F.* Species of relatively common occurrence above 150 fathoms. . . *S. lyra.*  
*FF.* Species whose occurrence above 150 fathoms is exceedingly rare . . . . . *S. planktonis.*  
*G.* Species never occurring above 50 fathoms. . . . . *K. subtilis.*  
*GG.* Species never occurring above 25 fathoms . . . . . *E. hamata.*  
*GGG.* Species occurring at irregular times above 25 fathoms, and sometimes even on the surface . . . . . *S. serratodentata.*

It is unnecessary to state that this key is not published for the purpose of furnishing a ready means of identifying the various species of Chætogonatha. Perhaps, when all the species from the four quarters of the globe have been studied as critically in regard to their behavior and ecological relations as they have in regard to their morphology, it will be possible to construct a ready means of identification on such a basis, but at present we can do no more than point out that the key does work for the San Diego region and ascertain what this fact signifies.

Its primary significance is that species are quite as distinguishable from their manner of distribution as from their morphological characteristics. In other words, each species has its own definite and distinctive mode of behavior and each adapts itself to the hydrographic and other elements of its environment in quite as definite a way as any of the other species.

This being true, the question at once arises: To what extent are morphological differences between the species proportional to, or correlatable with, their distributional differences. Ritter ('09) has pointed out that, if "change of environment and of environed organism are wholly and inseparably linked together," one ought to be able to measure and correlate the differentials between organisms with the differentials between their environments. However, in attempting to find such a "necessary correlation" in the case of *Halocynthia johnsoni*, native to the San Diego region, and *H. hauster*, native to the Washington coast, the results were negative. It is un-

necessary to point out that this is an exceedingly important line of investigation, for, if change of environment and of environed organism are not *inseparably* linked together, the hypothesis of "natural selection," with its attendant hypotheses of "survival of the fittest," "struggle for existence," etc., are at stake. Ask yourself if it is not *a priori* impossible for any of these hypothetical factors to operate in the formation of species except on the basis of variations in structure which are *more or less* adapted to the conditions of existence in which an organism finds itself? Again, does not logic demand that, if isolation be a *necessary* cause of species formation, two *similar* species must occupy similar but not identical or vastly different environmental complexes, because both could not be *equally* adapted to the same conditions by virtue of their *organic difference* nor to radically different conditions by virtue of their *organic similarity*?

Such questions sufficiently indicate the importance of our inquiry regarding the relation between the morphological and distributional characteristics of species and in this connection the key reveals the fact that *those species having the most coincident vertical distribution are those having the greatest morphological difference*. In other words, when the Chætognatha of this region are classified in the usual taxonomic fashion, five groups can be distinguished, of which each group contains species having the same fundamental *morphological* characteristics; but, when classified according to similarities and differences in vertical distribution, the species constituting any one of the five groups are those differing from each other in fundamental *distributional* characteristics. We have, then, two methods of classification, one of which results in groups of similar morphological but dissimilar distributional species, while the other results in groups of similar distributional but dissimilar morphological species. To illustrate concretely, the groups resulting from each method of classification are tabulated below:

## Groups of Similar Distributional Species

Group 1	{ <i>S. enflata</i> <i>S. neglecta</i>
Group 2	{ <i>S. bipunctata</i> <i>S. hexaptera</i>
Group 3	{ <i>S. lyra</i> <i>S. planktonis</i>
Group 4	{ <i>S. serratodentata</i> <i>K. subtilis</i> <i>E. hamata</i>

## Groups of Similar Morphological Species

Group 1	{ <i>S. enflata</i> <i>S. hexaptera</i> <i>S. lyra</i>
Group 2	{ <i>S. bipunctata</i> <i>S. neglecta</i> <i>S. planktonis</i>
Group 3	{ <i>S. serratodentata</i> <i>K. subtilis</i>
Group 4	{ <i>E. hamata</i>

By referring to the key (p. 35) it will be seen that *S. enflata* is separable from *S. neglecta* only by the fact that the former occurs in large numbers while the latter occurs in small numbers. These two species then constitute Group 1 of similar distributional species, but, while *S. enflata* falls in Group 1 of similar morphological species, *S. neglecta* is found in Group 2. It will therefore be worth while to see just how extensively the one species is morphologically differentiated from the other. To this end I have arranged, in the following table, some of the most striking differences between the two species.

TABLE VIII

STRUCTURAL DIFFERENCES BETWEEN *Sagitta enflata* AND *Sagitta neglecta*

Structures	<i>Sagitta enflata</i>	<i>Sagitta neglecta</i>
Collarette.	Entirely wanting.	Extending nearly to the ventral ganglion.
Anterior fin.	Separated from ventral ganglion by an interval of 17-26 per cent. of total length of animal.	Extends to the ventral ganglion.
Length of anterior fin.	7.4-15.9 per cent of total length of animal.	18-23 per cent. of total length of animal.
Length of posterior fin.	12-18 per cent. of total length of animal.	21-26 per cent. of total length of animal.
Extent of posterior fin.	Not more than half way from tail-septum to seminal vesicles.	To seminal vesicles.
Per cent. of posterior fin in front of tail-septum.	More than 50.	Less than 50.
Appearance of body.	Very transparent.	Opaque.
Width of body.	7-12 per cent. of total length of animal.	4.2-6.4 per cent. of total length of animal.

Muscles.	Weak and thin.	Strong and thick.
Lateral fields.	Very large.	Very small.
Length of tail.	16-24 per cent. of total length of animal.	26-30 per cent. of total length of animal.
External process of vestibular ridge.	At least 10 times longer than broad.	Not over 4 times longer than broad.

Doubtless the number of differences could be increased were we to search details, but the twelve set forth in the above table sufficiently emphasize the fact that the two species are fundamentally distinct from a morphological point of view. It would, in fact, be difficult to find any species within the genus more differentiated from *S. enflata* than is *S. neglecta*.

Looking to Group 2 of similar distributional species and referring to the key (p. 35) we find that *S. bipunctata* is separable from *S. hexaptera* only by virtue of occurring in large numbers and maintaining its maximum abundance above 25 fathoms, whereas *S. hexaptera* occurs in small numbers and maintains its maximum abundance below 40 fathoms. In contrast to this we find that, while *S. hexaptera* occurs in Group 1 of similar morphological species, *S. bipunctata* occurs in Group 2. The following table, therefore, reveals their most fundamental structural differences.

TABLE IX

STRUCTURAL DIFFERENCES BETWEEN *Sagitta bipunctata* AND *Sagitta hexaptera*

Structures	<i>Sagitta bipunctata</i>	<i>Sagitta hexaptera</i>
Collarlette.	Conspicuous but not extensive.	Entirely wanting.
Length of body.	12-17 mm. when mature.	24-55 mm. when mature.
Width of body.	5-7 per cent. of length.	7.3-11 per cent. of length.
Length of anterior fin.	15.9-23.7 per cent. of total length of animal.	8.6-11.8 per cent. of total length of animal.
Interval between anterior fin and ventral ganglion.	5-9 rarely 10 per cent. of total length of animal.	11.5-18.5 per cent. of total length of animal.
Extent of posterior fin.	To seminal vesicles.	Never to seminal vesicles.
Vestibular ridge.	Provided with the usual skeletal parts.	Without the usual skeletal parts.
Anterior teeth.	5-7 in number.	2-3 in number.

Posterior teeth.	12-14 in number.	2-4 in number
Seizing jaws.	Without crest.	Provided with short massive crest.

This table shows similar and just as fundamental morphological distinctions as those found between *S. enflata* and *S. neglecta*.

Group 3 of similar distributional species is composed of *S. lyra* and *S. planktonis*, and on referring to the key (p. 36) we see that the two species are distinguishable only by the fact that *S. lyra* is of relatively common occurrence above 150 fathoms. However, we find that *S. lyra* is placed in Group 1 of similar morphological species, while *S. planktonis* is placed in Group 2. The following table reveals the main morphological differences between the two species.

TABLE X

STRUCTURAL DIFFERENCES BETWEEN *Sagitta lyra* AND *Sagitta planktonis*

Structures	<i>Sagitta lyra</i>	<i>Sagitta planktonis</i>
Collarette.	Entirely wanting.	Massive, extending to ventral ganglion and anterior fin.
Body.	Translucent, nearly transparent. Tumid, but not retaining its form well.	Exceptionally opaque. Firm and rigid, retaining its form almost perfectly.
Muscles.	Weak and thin.	Strong and thick.
Length of anterior fin.	31.4-44.5 per cent. of total length of animal.	18.8-27 per cent. of total length of animal.
Relation of anterior fin to posterior fin.	Confluent.	Separated by an interval of 8-11 per cent. of total length of animal.
Extent of posterior fin.	To seminal vesicles.	Never to seminal vesicles.
Length of tail.	15.6-24.8 per cent. of total length of animal.	24-38 per cent. of total length of animal.
Lateral fields.	Large.	Very small.
Vestibular ridge.	Skeletal parts missing.	Skeletal parts well developed.
Posterior teeth.	3-9, rarely 10 in number.	11-15 in number.

Here again we find that there is no question concerning the great morphological difference between these two similar distributional species.

Finally we find that Group 4 of similar distributional species consists of *S. serratodentata*, *K. subtilis*, and *E. hamata*, and by referring to the key (p. 36) we see that they are separable only by the fact that *S. serratodentata* occurs to some extent above 25 fathoms, while *E. hamata* never occurs above this depth, and *K. subtilis* never occurs above 50 fathoms. Yet, we have as members of this group three species *belonging to three genera*, so that there can be no question regarding their fundamental morphological difference.

In what way then do these facts answer our question: "To what extent are morphological differences between species proportional to, or correlatable with, their distributional differences?" It is obvious that the only reply permitted by our data is that there is a *very definite correlation*, but one that is the *exact reverse* of what would *a priori* be expected on the basis of the Darwinian theory of "natural selection"; namely, that the morphological difference between two species is *inversely* proportional to their distributional difference, or, to state it otherwise, the coefficient of correlation between morphological and distributional differences among species approximates closely to  $-1$ .

#### RELATION BETWEEN SPECIES OBTAINED IN THE SAME HAULS WITH RESPECT TO SEXUAL MATURITY

Under this head it is proposed to briefly consider the evidence of physiological isolation or coincidence between species relative to their maturity in those cases where two or more were obtained in a single haul. It is obvious that open vertical and vertical closing net hauls do not yield data relevant to this question, for the reason that the vertical distance covered is so great (25 fathoms or more) that it is impossible to tell whether the specimens of two or more species were taken from the same depth or not. Concerning the horizontal hauls, however, this objection can not be made, and when they are examined we find that only 14 out of 148 surface hauls and 23 out of 108 closing-net hauls obtained more than one species.

TABLE XI  
SURFACE HAULS THAT OBTAINED MORE THAN ONE SPECIES

Haul No.	Species Obtained	No. of Specimens Obtained	Stage of Maturity
216	<i>S. bipunctata</i> . . . . .	200	Over 50 fully mature
	<i>S. hezaptera</i> . . . . .	2	Both small and very immature.
411	<i>S. enflata</i> . . . . .	3,500	Over half fully mature.
	<i>S. neglecta</i> . . . . .	9	One nearing, but none fully mature.
	<i>S. bipunctata</i> . . . . .	75	All small and very immature.
	<i>S. serratodentata</i> . . . . .	1	Very immature, ovary barely visible.
	<i>P. draco</i> . . . . .	1	Very immature, ovary not visible.
412	<i>S. enflata</i> . . . . .	3,100	Many fully mature.
	<i>S. hezaptera</i> . . . . .	4	All small and very immature.
	<i>S. serratodentata</i> . . . . .	1	Very immature, ovary barely visible.
	<i>S. bipunctata</i> . . . . .	64	All small and immature.
	<i>S. neglecta</i> . . . . .	75	None even approaching maturity.
473	<i>S. enflata</i> . . . . .	6	One mature, the rest nearly so.
	<i>S. neglecta</i> . . . . .	38	All immature.
	<i>S. bipunctata</i> . . . . .	6	One nearly mature, the others clearly immature.
1,416	<i>S. enflata</i> . . . . .	1	Nearly but not quite mature.
	<i>S. bipunctata</i> . . . . .	1,620	All stages, many fully mature.
1,422	<i>S. bipunctata</i> . . . . .	9	Several stages, one fully mature.
	<i>S. planktonis</i> . . . . .	1	Very immature, ovaries invisible.
1,426	<i>S. serratodentata</i> . . . . .	10	All small and immature.
	<i>S. bipunctata</i> . . . . .	1,250	All stages, many fully mature.
1,582	<i>S. serratodentata</i> . . . . .	7	All small and immature.
	<i>S. bipunctata</i> . . . . .	600	All stages, 25 mature or nearly so.
1,591	<i>S. serratodentata</i> . . . . .	5	All small and immature.
	<i>S. bipunctata</i> . . . . .	200	All stages, but mostly immature.
1,605	<i>S. serratodentata</i> . . . . .	1	Small and very immature.
	<i>S. bipunctata</i> . . . . .	35	Mostly immature.
1,686	<i>S. hezaptera</i> . . . . .	1	Small and very immature.
	<i>S. bipunctata</i> . . . . .	1,600	All stages, over 200 fully mature.
1,716	<i>S. serratodentata</i> . . . . .	1	Small and very immature.
	<i>S. bipunctata</i> . . . . .	50	Mostly immature, one fully mature.
1,738	<i>S. serratodentata</i> . . . . .	14	All small and immature.
	<i>S. bipunctata</i> . . . . .	105	All stages, some fully mature.
1,772	<i>S. serratodentata</i> . . . . .	1	Small and immature.
	<i>S. bipunctata</i> . . . . .	9	All small, none fully mature.

Concerning the 14 surface hauls, the following table reveals the fact that in only one haul (1,416) were representatives of two species taken which were nearly mature, and in this case the one specimen of *S. enflata*

did not appear to be fully mature. In every other haul only one species was represented by sexually mature individuals.

The following table, which contains data relative to hauls made with horizontal closing nets, shows no instance of two species having been taken in the same haul both of which were represented by sexually mature individuals.

The facts revealed in Tables XI and XII, when taken together with the foregoing discussion of vertical distribution, suggest that the various species reach maturity for the most part during different seasons, and that fertilization probably takes place in different strata of water according to the species. In the case of *S. enflata*, for instance, fertilization unquestionably takes place between the surface and ten fathoms and then only during the winter, if at all, in the San Diego region. With *S. bipunctata*, on the other hand, evidence is at hand [see Michael ('11)], which space forbids presenting here, showing that the species maintains a "center of migration" between 15 and 20 fathoms, from which center the species moves up and down in response to variations in light, temperature, salinity and other factors of its environment, which facts indicate that fertilization is mainly, if not exclusively, confined to this depth of 15 to 20 fathoms. In the case of *S. hexaptera* only the immature have been taken above 50 fathoms, which shows that fertilization must take place below this depth. Again, only the very immature of *S. serratodentata* have been taken above 100 fathoms, except at night when the larger specimens ascend to 50 fathoms. Similarly with *S. lyra*, the larger more nearly mature specimens do not occur above 200 fathoms to any extent, and so on with the other species.

It is quite true that much more knowledge is needed concerning the vertical distribution of most of the species before positive conclusions relative to the depth at which fertilization occurs can be advanced. Were the deeper water (below 350 fathoms) thoroughly investigated, dif-

TABLE XII

HORIZONTAL CLOSING NET HAULS THAT OBTAINED MORE THAN ONE SPECIES

Haul No.	Depth in Fathoms	Species Obtained	No. of Specimens Obtained	Stage of Maturity
1,873	5	<i>S. lyra</i> .....	1	Small and very immature.
		<i>S. bipunctata</i> .....	5	3 fully mature, 2 immature.
1,877	15	<i>S. serratodentata</i> ....	4	All small and immature.
		<i>S. bipunctata</i> .....	6	All small and immature.
1,748	25	<i>S. lyra</i> .....	5	All very small and immature.
		<i>S. serratodentata</i> ....	6	One nearly mature, the rest very immature.
		<i>S. bipunctata</i> .....	4	Small and remote from maturity.
1,761	25	<i>S. lyra</i> .....	1	Very small and immature.
		<i>S. bipunctata</i> .....	1	Nearly but not fully mature.
1,851	25	<i>S. serratodentata</i> ....	7	All small and immature.
		<i>S. bipunctata</i> .....	2	Nearly but not fully mature.
1,858	35	<i>S. serratodentata</i> ....	2	Small and immature.
		<i>S. bipunctata</i> .....	1	Nearly but not fully mature.
1,476	50	<i>S. hexaptera</i> .....	1	Remote from maturity.
		<i>S. bipunctata</i> .....	300	All stages, several mature.
		<i>S. planktonis</i> .....	1	Remote from maturity.
1,575	75	<i>S. serratodentata</i> ....	76	Mostly large and nearly mature.
		<i>S. bipunctata</i> .....	65	? ? ? ? ?
1,688	100	<i>S. lyra</i> .....	4	Very small and immature.
		<i>S. serratodentata</i> ....	4	One nearly mature, the rest remote from maturity.
1,714	100	<i>S. lyra</i> .....	1	Small and immature.
		<i>S. serratodentata</i> ....	9	One nearly mature, the rest small and immature.
1,757	100	<i>S. lyra</i> .....	1	Large and nearly mature.
		<i>S. bipunctata</i> .....	2	? ? ? ? ?
1,813	100	<i>S. lyra</i> .....	2	Large but not mature.
		<i>S. serratodentata</i> ....	12	All large but none fully mature.
1,979	100	<i>S. lyra</i> .....	1	Large but not mature.
		<i>S. serratodentata</i> ....	30	All stages, none fully mature.
1,927	125	<i>S. lyra</i> .....	11	All stages, two nearly mature.
		<i>S. serratodentata</i> ....	21	All large, none fully mature.
		<i>S. planktonis</i> .....	1	Small and very immature.
1,735	160	<i>S. lyra</i> .....	1	Small and very immature.
		<i>S. serratodentata</i> ....	16	All large and nearly mature.
1,926	200	<i>S. lyra</i> .....	13	All stages, none fully mature.
		<i>S. serratodentata</i> ....	46	All stages, some nearly mature.
		<i>S. planktonis</i> .....	1	Large but very immature.
		<i>K. subtilis</i> .....	3	Very immature.

Haul No.	Depth in Fathoms	Species Obtained	No. of Specimens Obtained	Stage of Maturity
1,948	200	<i>S. lyra</i> . . . . .	2	Large but not mature.
		<i>S. serratodentata</i> . . . . .	13	Large, some nearly mature.
1,978	200	<i>S. lyra</i> . . . . .	1	Large but not mature.
		<i>S. serratodentata</i> . . . . .	29	Large and nearly mature.
		<i>K. subtilis</i> . . . . .	1	Very immature.
1,732	220	<i>S. lyra</i> . . . . .	1	Large but immature.
		<i>S. serratodentata</i> . . . . .	13	Large and nearly mature.
1,557	250	<i>S. lyra</i> . . . . .	50	All stages, several nearly if not fully mature.
		<i>S. serratodentata</i> . . . . .	24	Large but immature.
1,729	250	<i>S. lyra</i> . . . . .	2	Small and immature.
		<i>S. serratodentata</i> . . . . .	17	Large, some nearly mature.
1,550	350	<i>S. lyra</i> . . . . .	2	Large but not mature.
		<i>S. planktonis</i> . . . . .	3	Large and nearly mature.
1,567	350	<i>S. serratodentata</i> . . . . .	2	Small and immature.
		<i>E. hamata</i> . . . . .	2	Large and nearly mature.

ferentials would undoubtedly be established between *S. lyra* and *S. planktonis* with reference to their depths of maximum abundance. Again, more extensive data relative to all depths, by increasing the number of specimens and hauls with which to deal, would enable us to split the region of 250 to 350 fathoms, for instance, and thus distinguish strata and establish specific differences within much smaller limits. However, on the basis of data already accumulated, all the evidence points toward the probability that the fertilization of each species normally takes place within the limits of its depth of maximum abundance.

#### SUMMARY AND GENERAL SIGNIFICANCE OF THE DATA

In the foregoing pages the following facts relative to the question of isolation and coincidence have been revealed:

1. Of the most closely related "couplets" of species only one occurs in the San Diego region, except in the case of *S. enflata* and *S. hexaptera*, the former of which can not be regarded as resident in this vicinity.

2. The general distribution of each member of a "couplet" is never entirely coincident with that of the other, but varies from a contiguous and overlapping to a radically isolated distribution, according to the "couplet."

3. Each species occurring in the San Diego region has its own definite and specific manner of vertical distribution just as truly as it has its own specific morphological characteristics.

4. Those San Diego species having the most similar vertical distribution are those possessing the most distinctive morphological characteristics or, to state it otherwise, the morphological difference between species is inversely proportional to their distributional difference.

5. Whenever two or more species have been obtained in the same haul, never more than one was represented by sexually mature individuals.

6. With one or two *possible* exceptions, the mature specimens of each species occur in different strata of water.

On the basis of these facts we are forced to conclude (a) that the more closely related species of Chaetognatha are isolated from each other either horizontally, vertically or by virtue of physiological differences causing fertilization to take place in different strata of water, and (b) that "Jordan's Law" is only partly true, when tested by vertical distribution, for, while the more closely related species do not inhabit the *same* environment, they do inhabit the most *remote* environments.

Aside from these obvious conclusions the primary significance of this paper is that of emphasizing the need of more *exhaustive* and *quantitative* data relative to organisms, on the one hand, and their environments, on the other, before any *solid* basis can be had upon which to build theories regarding the operation of isolation, adaptation, natural selection, mutation and other factors supposedly concerned in the evolution of species. The

existence of this need relative to pelagic organisms and their conditions of vertical distribution is readily recognized and our first impression may be that the extent of this *particular* need is exceptional, but an acquaintance with the literature on evolution shows plainly that the need is very general. Indeed, this literature is fairly bulging with evidences of mimicry, protective coloration, natural selection, etc., based upon an abundance of data concerning many organisms as well as their environments, which data, while supporting the hypotheses, rarely include any facts relative to the *essentially quantitative* nature of either the organisms or the environments investigated. The mere fact that this sort of data supports a hypothesis and that the logic is sound is not *adequate scientific* proof that the hypothesis is true, for, as Pearl ('11) and others have demonstrated, *logic may carry conviction, be supported by numerous data, and still prove erroneous when the quantitative relations of the facts included in such data are considered.* Therein lies the mischief of much of our *a priori* reasoning relative to evolution, namely, that it causes us to depend so largely upon *logic* that we overlook or neglect as insignificant the quantitative nature of organisms and particularly of environments. Our most urgent present need, therefore, is not so much the accumulation of additional *qualitative* data as it is an *exhaustive* and *quantitative* treatment of those facts now at hand.

While the biometrician and, to some extent, other students of evolution are treating their data quantitatively, the ease with which large numbers of individuals of pelagic species may be obtained without apparently diminishing the supply, gives an unusual opportunity to the marine biologist for applying quantitative methods on an extensive scale to many of the important problems of evolution. If all the planktological expeditions would join hands by publishing *all the data* relative to *every* haul (those that did not as well as those that did contain the species or group under consideration) and by recording the approximate, if not the exact, number of speci-

mens of each species obtained, instead of publishing only data relative to successful hauls and recording the species as abundant or rare, many problems now so largely discussed from hypothetical points of view could be analyzed entirely on a *factual* basis without involving committal to any hypothesis whatsoever. For instance, by such means it would be possible:

1. To measure the degree of variation in the *habits* of distribution of species.

2. To measure the extent of correlation between variation in the vertical distribution of species and variation in their horizontal distribution.

3. To measure the degree of correlation between morphological and ecological characteristics of species, and so arrive at an accurate analysis of the causes of adaptation.

4. To measure the *range* of adaptation accompanying the same structures.

5. To measure the *range* of variation in structure adapted to the same environmental conditions.

6. To analyze the *natural* behavior of a species without involving the necessity of first placing collected individuals under the artificial conditions of the laboratory and then reading the results, arrived at by experiment, back into their natural environment. I do not wish to minimize in the least the immense value of laboratory experiments on behavior, but, no matter how great the achievement, such experiments can not afford a reliable basis for interpreting the *natural* behavior of a species until it becomes possible to re-create nature in miniature.

While these are but a few of the problems that are urgently calling for solution, I can not help but feel that, in the foregoing pages, we have touched the fringe of a line of quantitative investigation destined to yield much of importance to the student of evolution.

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## A FAMILY OF SPOTTED NEGROES

Q. I. SIMPSON AND W. E. CASTLE<sup>1</sup>

It is the purpose of this note to put on record an interesting variation in human skin color which made its appearance as a mutation or sport in a negro family of the southern United States some sixty years ago and has shown itself fully hereditary through two generations of offspring. The nature of the variation is shown in Figs. 1-4. It consists of a "piebald" condition of the skin, which is spotted with white in a fairly definite pattern, not<sup>2</sup> unlike that of certain domesticated animals. A more-or-less continuous white area begins on the top of the head, which has a crest of white hair, extends down over the face (where, however, it may be interrupted) and broadens out on the chest, which is either entirely white or finely mottled. In the whitest individuals the chest area extends around the sides of the body on to the back (see Fig. 4), but fails to reach the mid-dorsal line. It also extends on to the arms in like proportion to its extension elsewhere on the body, but the lower forearm and hands, like the feet, are in all observed cases dark. The ventral white area continues downward from the waist line, and in at least one case (Fig. 4) covers the legs, which are nearly free from black spots down to the knees. There larger and more numerous specks of black begin, which become continuous above the ankles.

If we should describe the pattern in terms of its black

<sup>1</sup> The material on which this paper is based was collected by the senior author; the junior author has merely assisted in preparing the material for publication.

<sup>2</sup> A photograph in our possession of the same four individuals shown in Fig. 1 together with the father of the three children, taken when the children were small, but now too faded for successful reproduction, makes it clear that the pigmented areas have not changed in position during the intervening period. As in other piebald mammals the pigmented areas have definite boundaries fixed at birth and not subsequently changeable.

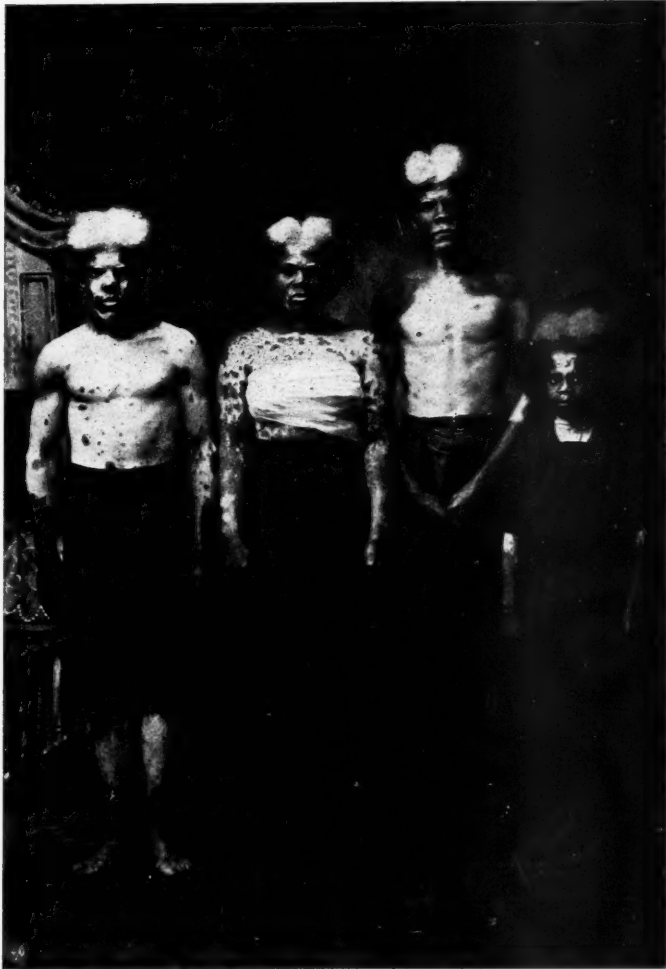


FIG. 1. Mrs. Eliza D., her sons Jim and Robert (the taller one) and daughter, Lillie. Photographed 1910.

areas, we should mention as its most prominent feature the *back-stripe* (Fig. 4) which begins on the head and extends the entire length of the trunk, narrowing below and ending on the buttocks. In the taller son, Robert,



FIG. 2. Back view of Mrs. Eliza D., seen in front view in Fig. 1.

and states positively that there were no spotted negroes previously in that region. The colored skin of Mrs. S. A. is "medium dark" as is that of her husband, who is entirely normal in appearance, being free from spots.

The pair were married in 1868 and have had fifteen children, all of whom are living, a fact which indicates a healthy vigorous stock. Of the children eight are spotted like the mother, the remaining seven being normal, without spots, but varying in

Fig. 1, the back-stripe is so wide that it covers the sides of the body also.

The original mutant, founder of this line of spotted negroes, Mrs. S. A., is still living. She was born in 1853 in Louisiana, both her parents being normally colored negroes, the father "dark," according to the statement of her husband who grew up in the same neighborhood



FIG. 3. Lillie, daughter of Mrs. Eliza D. Compare Fig 1.

depth of pigmentation, as is usual in mulatto families. The pigmentation of spotted children and grandchildren



FIG. 4. Back view of Jim, seen in front view, at the left of Fig. 1.

likewise varies in intensity from light mulatto to coal black. The white spots are however in all cases entirely devoid of pigment.

Six of the fifteen children of Mr. and Mrs. S. A., three normal and three spotted, married normal negro mates and have had from two to four children each. The normals have had only normal children, in all seven. The spotted ones have had nine spotted and two normal children.

The normal children of Mr. and Mrs. S. A. who married consisted of two daughters and one son; the spotted ones consisted of two sons and one daughter. There is evidently no sex-limitation in the transmission of the spotted pattern, which behaves consistently as a simple Mendelian dominant character, the only peculiarity of the case being the excess of spotted grandchildren over the expected one half. But this quite probably is a chance deviation due to the small numbers under consideration, or to failure to secure as complete a report of the unspotted as of the spotted grandchildren.

The descendants of Mr. and Mrs. S. A. are now widely scattered through the United States and Europe, certain of the spotted ones being connected with "museums." Their peculiarity is therefore an economic asset and not likely to interfere with their racial increase. The individuals thus far produced are clearly from their parentage all heterozygous for the spotted character, which they transmit in half only of their germ-cells. If in the course of time two spotted individuals of this race, not closely related, should marry each other, we might on Mendelian principles expect the production of a new type of individual, one homozygous in spotting, which would transmit the character in *all* its germ-cells. What the *somatic* character of such an individual would be we can at present only conjecture. Our experience with the domesticated animals leads us to think that it certainly would not be an albino with pink eyes and unpigmented or faintly pigmented skin, since true albinism is genetically entirely distinct from spotting with white and is recessive in heredity whereas this character is dominant. More likely it would resemble "black-eyed whites" such

as occur among mice, rabbits, guinea-pigs, cats, dogs, cattle and horses. Our experience with these animals would lead us to expect that the homozygote in this strain of spotted negroes would be either wholly white, that is, with snow-white skin and hair but with colored eyes, or spotted but with pigmented areas still further reduced in extent than in the heterozygote. Some student of genetics generations hence may be able to answer the question. To this end we shall deposit with the Eugenics Record Office at Cold Spring Harbor, N. Y., our original data including the correct names and present whereabouts of these people.

Three of the spotted children of this family, of whom we have been unable to secure pictures, are undoubtedly identical with "The Three Striped Graces" figured (Plate VV) and described (p. 248) by Pearson, Nettleship and Usher in "A Monograph of Albinism in Man," London, 1911, after Hutchinson, *British Medical Journal*, June, 1910, p. 1480. The names given by Pearson, *et al.*, for the three individuals are "Mary, Rose and Fanny," which agree sufficiently well with individuals VII, VIII and X, of our table. Our own information obtained from members of the family indicates that *at present* VII is in America, while VIII, X and XIV together with the grandchild, Beatrice, are in Europe.

TABLE

DESCENDANTS OF MR. AND MRS. S. A., THE FORMER A NORMAL,  
THE LATTER A SPOTTED NEGRO

<i>Children</i>	<i>Grandchildren</i>
I. Mrs. Eliza D., spotted, Figs. 1 and 2; Mate, mulatto.	1. Spotted son (dead); 2. Spotted, Jim (pigment dark), Figs. 1 and 4; 3. Spotted, Robert (pigment light), taller son, Fig. 1; 4. Spotted, Lillie (pigment me- dium dark), Figs. 1, right, and 3.
II. Mrs. Eugenia —, normal; Mate, colored.	Two normal.

- |   |  |
|---|--|
| III. Mr. Horace A., spotted;<br>First mate, light mulatto;<br><br>Second mate, black. | 1. Normal, light brown;<br>2. Spotted, brown;<br>3. Spotted, brown;<br>1. Spotted, black.<br>Three normal. |
| IV. Mr. Jake A., normal;<br>Mate, colored.  |  |
| V. Mr. John A., spotted;<br>Mate, dark.   | 1. Spotted, Beatrice;<br>2. Normal;<br>3. Spotted.<br>Two normal.  |
| VI. Mrs. Jane —, normal;<br>Mate, colored.  |  |
| VII. Marie, spotted.  |  |
| VIII. Rosa, spotted.  |  |
| IX. Dolphus, normal.  |  |
| X. Fannie, spotted.   |  |
| XI. Maggie, normal.   |  |
| XII. Bennie, spotted.   |  |
| XIII. Louis, normal.  |  |
| XIV. Sadie, spotted.  |  |
| XV. Hattie, normal.   |  |

# THE EFFECT OF FERTILIZERS ON VARIATION IN CORN AND BEANS

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THE data here reported were secured in the summer of 1909 from a field of sweet corn and beans which were fertilized with nitrogen phosphorus and potash separately and in combination after the manner described later. The original purpose of the investigation was to determine if the differences caused by fertilization were in any degree transmitted to succeeding generations. Owing to development of other work it has been impossible to carry this on as planned. It is thought that the data secured may have sufficient interest and value to warrant their presentation.

The plot of land used appeared much exhausted of both plant food and humus. It had previously been used as a raspberry patch. It lay on a gentle southeastern slope sheltered on the opposite side by a belt of woods which, however, was far enough distant to prevent injury from shade or root trespass.

The field was rectangular in shape, 300 feet long and 60 feet wide. It was divided crosswise into twelve plots, each 25 × 60 feet. The fertilizers and their amounts were as follows:

Plot	Lbs.	Plot	Lbs.
1. Nitrate of Soda .....	12	10. Check	
2. Check		11. { Nitrate of Soda .....	12
3. { Nitrate of Soda .....	12	{ Acid Phosphate .....	30
{ Acid Phosphate .....	30	{ Sulphate of Potash .....	8
4. Acid Phosphate .....	30	{ Manure .....	500
5. { Acid Phosphate .....	30	12. { Sulphate of Potash .....	10
{ Sulphate of Potash .....	8	{ Acid Phosphate .....	40
6. Check		{ Nitrate of Soda .....	16
7. Sulphate of Potash .....	8		
8. { Nitrate of Soda .....	12		
{ Sulphate of Potash .....	8		
9. { Nitrate of Soda .....	8		
{ Acid Phosphate .....	20		
{ Sulphate of Potash .....	6		

	Beans	Corn
1	Nitrate 12 lbs 30'	of Soda 12 lbs 30'
2	Check	
3	Nitrate of Acid Phosphate 30 lbs	Soda 12 lbs Potash 8 lbs
4	Acid Phosphate 30 lbs	
5	Acid Phosphate 30 lbs Sulphate	Potash 8 lbs
6	Check	
7	Sulphate	Potash 8 lbs
8	Nitrate of Sulphate	Soda 12 lbs Potash 8 lbs
9	Nitrate of Acid Phosphate 20 lbs Sulphate	Soda 8 lbs Potash 6 lbs
10	Check	
11	Nitrate of Acid Phosphate 30 lbs Sulphate	Soda 12 lbs Potash 8 lbs
12	Manure Nitrate of Acid Phosphate 40 lbs Sulphate	500 lbs Soda 16 lbs Potash 10 lbs

FIG. 1. Plan of Experimental Area.

It is seen that plots 1, 3, 4, 5, 7, 8 and 11 received the several fertilizing materials singly and in combination in what may be called normal amounts of 12 pounds nitrate of soda, 30 pounds acid phosphate and 8 pounds sulphate of potash; plot 9 received all these in considerably smaller amounts; while in plot 12 an excess of the chemicals was applied together with a liberal quantity of ordinary barnyard manure, the idea being to supply here a maximum of the stimulus that ordinary fertilizing materials may be expected to afford. The lower half of the entire plot was planted to corn and the upper half to beans. These facts are graphically shown in Fig. 1. One half of the nitrate and the entire amounts of the other materials were applied broadcast on June 8 and harrowed in. The corn was of the Red Cory variety and was planted June 14, and the Davis white wax beans the next day in drills running lengthwise of the area. Both were thinned where necessary to give the corn space of four inches and the beans three inches. The remainder of the nitrate was applied about three weeks after planting, but the exact date can not be given. The plants were cared for in the usual way and the measurements taken from September 14 to 16, or possibly a few days later. With the corn a record was made of the following: distance from ground to uppermost ear, distance from ground to lowest branch of tassel, and the number of ears formed. Where ear-bearing suckers

occurred, the same records were made in such a manner as to indicate their parent stalks. The plants on space of two feet on each end of the plots were omitted in the measurements.

TABLE I  
EFFECT OF FERTILIZER ON YIELD OF CORN

Plot	Total Stalks	Barren Stalks, Per Cent.	2-Eared Stalks, Per Cent.	Per Cent. Ear-bearing Suckers
1. Nitrate of soda.....	241	2.90	1.66	3.32
2. Check.....	248	43.15	.40	.40
3. { Nitrate of soda } { Acid phosphate }	281	5.34	4.27	7.47
4. Acid phosphate.....	244	44.26	.60	.41
5. { Acid phosphate } { Sulphate of potash }	229	35.37	.00	.87
6. Check.....	251	29.87	.00	.40
7. Sulphate of potash.....	314	28.03	.00	.64
8. { Nitrate of soda } { Sulphate of potash }	269	4.83	3.35	7.06
9. { Nitrate of soda } { Acid phosphate } { Sulphate of potash } ( $\frac{2}{3}$ normal)	255	9.80	1.57	5.88
10. Check.....	225	28.44	.44	.88
11. { Nitrate of soda } { Acid phosphate } { Sulphate of potash } (normal amounts)	241	7.05	3.73	10.37
12. { Nitrate of soda } { Acid phosphate } { Sulphate of potash } (in excess)	248	4.43	10.09	39.92
Manure				
Av. 3 Checks.....		33.82	.28	.56

Table I gives figures bearing on the productiveness of the corn, and indicates that the deficient element was nitrogen.<sup>1</sup> There is no indication that the addition of potash or phosphorus decreased the number of barren stalks at all, nor did either alone increase the number of two-eared stalks or ear-bearing suckers, though there appears to be considerable benefit from each when applied with nitrogen, and still more when all three are supplied. The addition of manure results beneficially in all ways, possibly on account of its physical action as well as by the direct addition of plant food.

<sup>1</sup> While the discussion following is in terms of the elements of fertility, it is of course possible that other carriers of the same elements might have given different results. It has seemed simpler to express the matter in terms of the elements and with a full reading of the text no misunderstanding on this point is possible.

TABLE II  
VARIATION IN STATURE OF CORN PLANTS

Plot	Ear Height			Stalk Height		
	Mean	Standard Deviation	Coefficient of Variability	Mean	Standard Deviation	Coefficient of Variability
1. Nitrate of soda	11.61 ± .19	4.20 ± .13	36.18 ± 1.26	46.68 ± .25	5.80 ± .18	12.42 ± .40
2. Check	11.78 ± .19	3.36 ± .14	28.52 ± 1.23	45.26 ± .29	6.72 ± .20	14.84 ± .46
3. { Nitrate of soda Acid phosphate }	13.18 ± .17	4.39 ± .14	33.37 ± 1.07	50.42 ± .25	6.14 ± .18	12.18 ± .35
4. Acid phosphate	12.00 ± .20	3.39 ± .14	28.25 ± 1.24	44.76 ± .29	7.07 ± .22	13.56 ± .48
5. { Acid phosphate Sulphate of potash }	11.69 ± .19	3.36 ± .13	28.75 ± 1.21	43.07 ± .31	7.03 ± .22	16.33 ± .53
6. Sulphate of potash	11.64 ± .16	3.22 ± .12	27.66 ± 1.07	45.71 ± .29	6.74 ± .20	14.72 ± .45
7. { Nitrate of soda Sulphate of potash }	12.61 ± .17	3.67 ± .12	29.02 ± .99	47.02 ± .27	7.16 ± .19	15.28
8. Nitrate of soda	13.53 ± .18	4.15 ± .12	30.45 ± .96	50.45 ± .28	6.84 ± .22	13.56 ± .40
9. { Acid phosphate Sulphate of potash }	13.02 ± .19	4.25 ± .13	32.64 ± 1.13	49.49 ± .30	7.05 ± .21	14.25 ± .43
10. Check	10.33 ± .16	3.28 ± .12	31.75 ± 1.31	42.12 ± .29	6.45 ± .21	15.31 ± .50
11. { Nitrate of soda Acid phosphate Sulphate of potash (normal amounts) }	13.37 ± .18	4.05 ± .13	30.29 ± 1.05	51.38 ± .30	6.98 ± .22	13.59 ± .44
12. { Nitrate of soda Acid phosphate Sulphate of potash (in excess) }	15.36 ± .22	4.97 ± .15	32.36 ± 1.10	56.65 ± .31	7.25 ± .22	12.80 ± .38
Manure						
Av. 3 Check	11.25	3.29	29.31	44.36	6.64	14.96

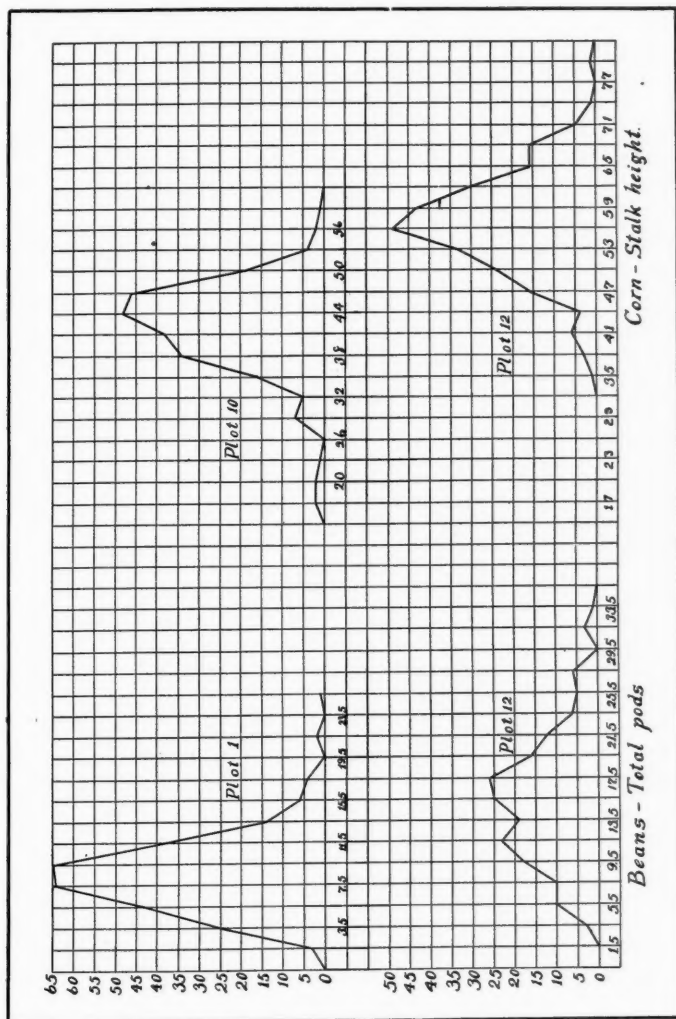


FIG. 2. Variation in Beans and Corn.

Table II shows the variation in stature of the corn plants. With respect to ear height it is seen that the addition of the mineral elements, especially if nitrogen was also supplied, apparently raised the mean. It will be remembered that ear height is taken to the uppermost ear in two-eared stalks, and a comparison with Table I indicates that the ear height is significantly greater only where there is a considerable percentage of two-eared stalks, making it very probable that none of the fertilizers influenced in any marked degree the height of the ear on single-eared stalks, or of the lower ear where two were present.

The differences in variability of ear height so far as they are significant are probably to be referred to the same cause, an increased number of two-eared stalks resulting in greater variability, as would be expected.

TABLE III  
VARIATION IN YIELD OF BEANS

Plot	Pods per Vine		Coefficient of Variability
	Mean	Standard Deviation	
1. Nitrate of soda . . . . .	8.63 $\pm$ .14	3.49 $\pm$ .10	40.441 $\pm$ 1.36
2. Check . . . . .	4.81 $\pm$ .14	3.18 $\pm$ .10	66.11 $\pm$ 3.21
3. { Nitrate of soda } . . . . .	9.62 $\pm$ .23	5.25 $\pm$ .16	54.42 $\pm$ 2.43
4. { Acid phosphate } . . . . .	7.61 $\pm$ .18	3.94 $\pm$ .13	51.77 $\pm$ 1.60
5. { Acid phosphate } . . . . .	10.71 $\pm$ .25	5.05 $\pm$ .17	47.15 $\pm$ 1.93
6. { Sulphate of potash } . . . . .	9.13 $\pm$ .22	4.34 $\pm$ .15	47.53 $\pm$ 2.02
7. Sulphate of potash . . . . .	10.09 $\pm$ .18	3.76 $\pm$ .13	37.26 $\pm$ 1.41
8. { Nitrate of soda } . . . . .	9.82 $\pm$ .16	3.59 $\pm$ .11	36.56 $\pm$ 1.30
9. { Sulphate of potash } . . . . .	12.26 $\pm$ .21	4.39 $\pm$ .15	35.79 $\pm$ 1.36
10. { Nitrate of soda } . . . . .	6.75 $\pm$ .16	2.96 $\pm$ .11	43.85 $\pm$ 1.93
11. { Acid phosphate } . . . . .	13.20 $\pm$ .21	5.01 $\pm$ .15	37.95 $\pm$ 1.30
12. { Sulphate of potash } . . . . .	15.34 $\pm$ .30	6.09 $\pm$ .22	38.38 $\pm$ 1.54
Av. 3 Check . . . . .	6.89	3.49	52.49

There is little evidence that either of the mineral elements alone or both together increased the stature of the whole plant,

though nitrogen did have this effect. Nitrogen together with either phosphorus or potash had a more pronounced effect, and when all three were applied together in plot 11 the stature was still greater. Increasing the amounts of the commercial fertilizers and adding manure in plot 12 gave still taller corn.

The standard deviation is apparently increased by the mineral elements either alone or together, while nitrogen operates to lessen this measure of variability. When all are used together both influences seem to operate and the standard deviation is increased, but not so much as with the mineral elements alone. The increase of the standard deviation where considerable amounts of complete fertilizer is added is not in proportion to the increased mean, and the coefficient of variability is lessened.

It was not found possible to make any measurements bearing on the vegetative vigor of the bean plants; the only figures available are those of yield as measured by the total number of pods on each plant. Table III indicates that potash was most effective in increasing the mean number of pods per vine, though it will be remembered that this element was of the least avail with corn. Nitrogen seems next, and there is a possible beneficial effect from phosphorus. When all are applied the average is higher even on the plot receiving only two thirds the normal amount. Increasing the quantity of chemicals and adding manure increase still further the yield. The results are not as consistent as in the case of stalk height of corn. This variability in yield finds further expression in the larger variation within each plot as expressed by the coefficients of variability which are nearly three times as great as those for stalk height of corn.

The effect of the single elements on the standard deviation is not very clear, but it seems that two or more together increase it, but if nitrogen is present this increase is not in proportion to the increased mean and the coefficient of variability is lessened. There is some indication that potash has a similar effect. Owing to the uncertainty of pod setting a great many data are necessary in order to give definite information on these points.<sup>1</sup>

In Fig. 2 is shown graphically the difference in the effect of the fertilizer on yield of beans and stalk height of corn. This shows that fertilizers greatly extended the range of variation of total pods per vine; the minimum is only slightly raised, but there are many more plants with a considerable number of pods and the maximum number of pods per vine too is markedly in-

creased. There is a greater "scatter" to the distribution. With the stalk height of corn the "scatter" is not much increased, but the whole polygon is moved bodily to a higher position. The fertilizer had a direct effect on every stalk of corn, increasing its stature, but it had little effect on the productiveness of a few of the bean plants, though increasing that of most of them.

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